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RESEARCH PAPER

CLASSIFICATION OF OPEN HABITATS IN THE PALAEARCTIC

Regional typology of spring vegetation in Parc Ela (Grisons, Switzerland)

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Abstract

Aims: The spring habitats of Central Europe are insular biotopes of high ecological value. Although subject to severe exploitation pressures, they do not yet have a comprehensive protection status in Switzerland. Contributing to this challenge is the controversy involved with their syntaxonomic classification. In the context of the development of a regional conservation strategy and the establishment of a national inventory of Swiss springs, we carried out a regional survey of spring vegetation and aimed to translate this into a classification system. **Study area:** Montane and subalpine zones of Parc Ela (Grisons, Switzerland). **Methods:** We selected 20 springs to cover different regions, elevations and bedrock types within the park. In each of them we recorded complete vascular plant and bryophyte composition as well as a range of environmental variables in three 1-m^2 plots that were placed to reflect the heterogeneity within the spring. After running an unsupervised classification with modified TWINSPAN, the distinguished vegetation units were characterized in terms of diagnostic species, species richness and environmental variables and placed within the syntaxonomic system. **Results:** Species richness was high (total species 264, mean 21.7 species in 1 m^2). The two most important environmental gradients of the ordination were elevation/water conductivity and insolation/water pH/soil reaction EIV. We distinguished seven communities within two main groups. **Conclusions:** All unshaded springs, including those over siliceous bedrock, could be assigned to a broadly defined *Cratoneurion*. The petrifying springs were not strongly distinguishable floristically from other base-rich springs. The forest springs, although often not clearly differentiated from their unshaded counterparts, could be provisionally divided into the alliances *Caricion remotae* and *Lycopodo europaei-Cratoneurion commutati*. As there is a certain threat to these habitats in the park due to anthropogenic influence, protection measures are recommended, most importantly the appropriate management of alpine pastures.

Taxonomic reference: Juillerat et al. (2017) for vascular plants, Meier et al. (2013) for bryophytes.

Abbreviations: ANOVA = analysis of variance; DCA = detrended correspondence analysis; EIV = ecological indicator value; FOEN = Federal Office of the Environment (Switzerland); NCHO = Ordinance on the Protection of Nature and Cultural Heritage; SD = standard deviation; TWINSPAN = Two Way Indicator Species Analysis; WPA = Federal Act on the Protection of Waters.

Keywords

bryophyte, helocrene, montane, *Montio-Cardaminetea*, Parc Ela, phytosociology, regional typology, rheocrene, spring vegetation, subalpine, Switzerland, unsupervised classification

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Introduction

Central European springs are small but complex island biotopes. Their unique environmental conditions exert great influence on the vegetation and allow colonization by many highly specialized organisms, including glacial relicts (Wilmanns 1998). Around the spring outlet, environmental conditions remain relatively constant over time: spring water temperature remains close to the annual mean air temperature (Pott and Remy 2000), and humidity near the surface of the substrate is high, but the substrate is rarely fully saturated (Zechmeister and Mucina 1994). Strong ecological gradients (Brunke et al. 2015) and spatial heterogeneity (Illies and Botosaneanu 1963; Weigand 1998) result in great species richness.

Because of these conditions, as well as their small size and relative isolation (Zollhöfer 1997; Weigand 1998), springs are sensitive habitats. Zollhöfer (1999) estimated that 95% of the springs on the Swiss Plateau had been tapped or otherwise impaired by 1999; this number has likely increased in the intervening 20 years. Specialized spring-habitat species are particularly disadvantaged by habitat degradation (Heino et al. 2005; Juutinen 2011). Threats also exist in the sparsely populated Alps, where springs contribute strongly to regional biodiversity (Reiss et al. 2016): in structural surveys of the springs in Parc Ela (Grisons, CH), 24% were classified as moderately to severely impaired (Küry 2020, unpublished). Although spring habitats are ecologically valuable and subject to strong anthropogenic pressures, they do not have a comprehensive protection status in Switzerland. Unshaded spring habitats are listed in the Ordinance on the Protection of Nature and Cultural Heritage (NCHO) as "habitats worthy of protection" (Annex 1 NCHO, see also Delarze et al. 2016), but this unfortunately offers only limited protection, e.g., that encroachment must meet "an overriding need" (Art. 14 NCHO). The provisions of the Water Protection Act implicitly apply to spring habitats (Art. 1–4 WPA), but this protection is "so broad and general as to be ineffective" (Zollhöfer 1997).

In order to develop a differentiated conservation strategy for springs, it would be useful to put spring habitats into a universal scheme. Although phytocoenoses are particularly useful as reference units for conservation (Dengler 2003), phytosociology has been of limited use for spring conservation to date because the class *Montio-Cardaminetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944 is fraught with controversy (e.g., Beierkuhnlein and Gollan 1999). The importance of insolation and water chemistry for species composition are particularly contentious points. The classification of spring habitats is even more challenging in the mountains, where the differences between hard- and soft-water springs are less pronounced (Braun-Blanquet 1949; Geissler 1976; Pott 1995; Pignatti and Pignatti 2014). In these habitats, local climatic conditions gain importance for the formation of spring vegetation (Beierkuhnlein and Gollan 1999).

Switzerland, unlike many other European countries or regions (e.g. Valachovič 2001; Berg et al. 2004; Chytrý 2011), lacks a data-based, country-wide syntaxonomic overview. For practical conservation purposes, parts of the TypoCH habitat typology (Delarze et al. 2015) have been adopted post-hoc into the List of Biotope Types deserving Protection (NCHO Annex 1) and other official documents. However, this typology is poorly resolved. The description of the base-rich and base-poor alliances *Cratoneurion commutati* Koch 1928 and *Cardamino-Montion* Br.-Bl. 1926 hardly reflect the geological complexity of Switzerland. Forest springs are not treated separately, but rather blanketly assigned to the forest association *Fraxinion* in agreement with Ellenberg and Klötzli (1972). Such forests hardly occur above the montane level; thus, the numerous springs within Swiss mountain forests are excluded from the classification system entirely.

In general, the distinction between springs and their contact associations is often ambiguous because of their strong spatial variation and interlock with adjacent habitats (Warncke 1980; Beierkuhnlein and Gollan 1999). There are few diagnostic plant species that are not also common in other habitats (e.g., fens) (Oberdorfer 1992; Beierkuhnlein and Gollan 1999), and spring habitats with similar environmental conditions often have very different species compositions, especially in the mountains (Cantonati et al. 2006). The following general methodological problems also arise in the syntaxonomic treatment of the *Montio-Cardaminetea*:

- Older typologies are usually not based on sufficiently large datasets (Dengler et al. 2005);
- The recording of bryophytes is rudimentary in some works;
- Most studies comprise geographically narrowly restricted regional surveys (Cantonati et al. 2006);
- Extreme variation in relevé size affects fidelity values (Dengler et al. 2009).

Due to these difficulties, there is a need for a Europe-wide systematic review of the class *Montio-Cardaminetea*, based on a comprehensive data basis. Hájek et al. started a project to this end in 2020 (pers. comm.). The data of this study will be included in Hájek's project.

Springs of the Swiss Alps have been the subject of various vegetation surveys, mostly in the context of regional studies of alpine vegetation in Grisons (Braun-Blanquet 1949; Trepp 1968) or of international studies of alpine springs (e.g. Sekulová et al. 2012). Other hydrobiological studies of Swiss springs do not comprise detailed vegetation surveys (e.g. Nadig 1942; Zollhöfer 1997). Geissler (1976) identified typical associations for the eastern part of the Swiss Alps, sampling in 27 localities and citing a gap in the otherwise thorough investigation of Swiss alpine vegetation which seems to have persisted to the present day. It is hoped that the records of this study contribute to a more complete understanding of spring vegetation in the Swiss Alps.

Parc Ela's plan to develop a conservation concept for their spring habitats, as well as the commission of a national inventory of spring habitats by the Federal Office for the Environment FOEN (Küry et al. 2019), provide the impetus for this work. To increase knowledge of spring habitats, Audorff et al. (2011) cite the importance of regional studies including physico-chemical parameters and multiple organism groups. Since the patterns of spring biodiversity differ greatly between mountain regions, local studies can also be helpful in identifying the relevant parameters (Sekulová et al. 2012). In this sense, this work aims to characterize the diversity of spring habitats in Parc Ela and identify the underlying environmental factors so that effective conservation measures can be developed.

Study area

As the largest nature park in Switzerland, Parc Ela covers 548 km² in the canton of Grisons (Figure 1). The park area includes the Surses and Albula valleys and the surrounding Albula, Plessur and Oberhalbsteiner Alps. As inner-alpine valleys in central Grisons, the Surses and Albula valleys have a continental climate (Figure 2). The year has up to 190 days of frost, which shortens the vegetation period to about 6 months.

The park is located on the Pennine and Eastern Alpine nappes, with the Surses valley lying in the middle. A large part of the park lies on basic bedrock, mainly biogenic sediments and evaporites (Federal Office of Topography swisstopo 2020). To the south, around the Albula, Septimer and Julier passes, sedimentary and crystalline rocks (granodiorite, gneiss) alternate on a small scale. In the valleys, especially in the Surses valley, alluvial debris and landslide deposits occur over large areas. The mountain landscape is glacially influenced, its soils shallow and young (ibid.). The springs of this study are located between 956 and 2,115 m a.s.l, as shown in Figure 1.

The park is only sparsely populated. Agricultural use consists mainly of alpine pasture. Park habitats include moorlands, heathland, mountain grasslands, and richly structured landscapes which had been historically cultivated for subsistence agriculture. Tourism is of great importance for the local economy and regional development.

Methods

Vegetation survey

Sites were selected in accordance with the presumed main environmental gradients of shading, elevation, and

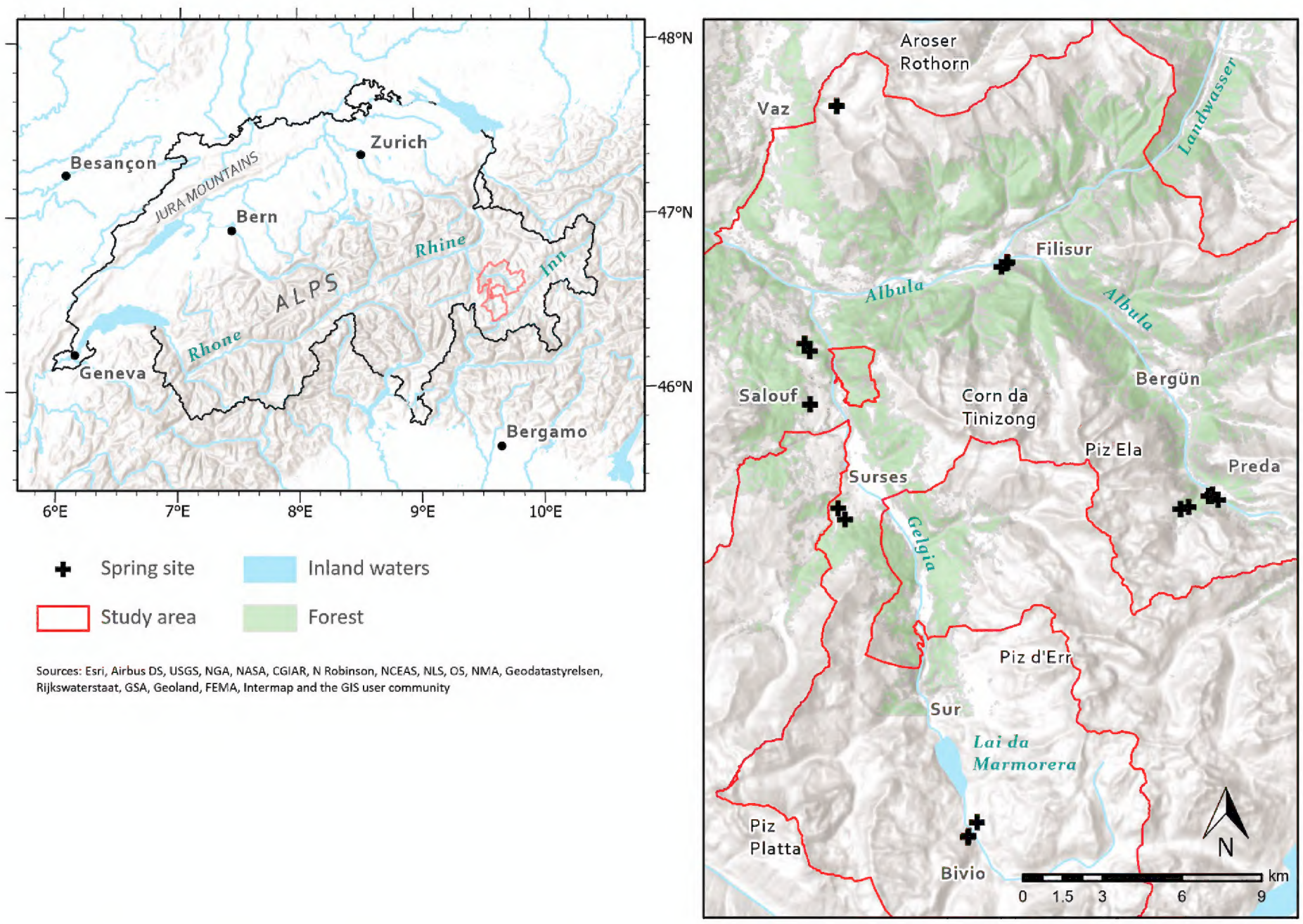

Figure 1. Maps of the study area. Left – location of Parc Ela in Switzerland; right – overview of all studied springs. Thematic layers by the Federal Office of the Environment FOEN and swisstopo.

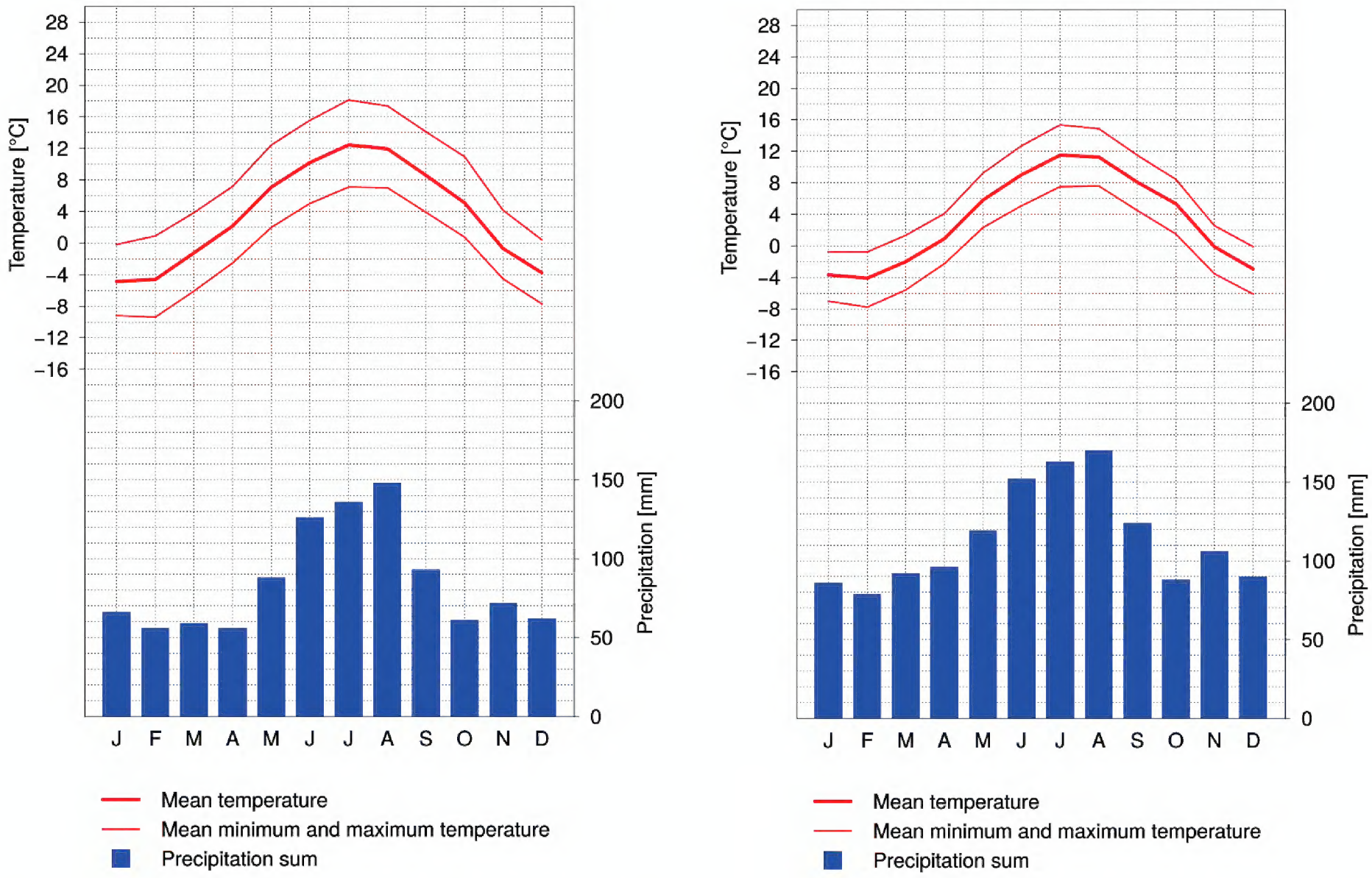

Figure 2. The climate at Arosa (1,878 m, left) and Davos (1,594 m, right) is taken as representative for central Grisons. The climate diagrams show mean values for the standard period 1981–2010. Annual precipitation Arosa 1,365 mm; annual mean temperature Arosa 3.6°C; annual precipitation Davos 1,022 mm; annual mean temperature Davos 3.5°C (Federal Office of Meteorology and Climatology MeteoSwiss 2020).

spring water chemistry. The cantonal spring inventory (GeoGR 2020) was used as a basis, as well as data from the structural surveys of the springs of the Grisons parks 2016–2018 (Küry 2020, unpublished). Sites of natural to semi-natural quality with high or medium conservation priority were preferred. Each spring was assigned a hydrologic type based on the Steinmann-Thienemann concept (Steinmann 1915; Thienemann 1922); in some cases, springs were assigned to the so-called linear or wandering type (Zollhöfer 1997; Küry et al. 2019). Because natural limnocrenes are rare in the region, they were omitted from the study.

Vegetation surveys were conducted in July and August 2020. Three plots (relevés) of 1 m^2 were recorded per spring site, arranged to best cover the variability evident in the field. Although single plots were intended to be as homogeneous as possible, neither ostensibly "fragmentary" nor "atypical" sites were excluded from the surveys in order to capture the real situation as completely as possible (Dengler et al. 2005). All vascular plants and bryophytes were recorded, with percent cover as importance measure. The nomenclature followed Juillerat et al. (2017) for vascular plants and Meier et al. (2013) for bryophytes. Vascular plants were determined using works by Hess et al. (2015) and Eggenberg and Möhl (2013). For the bryophyte determinations, the following works were drawn upon: Burck (1947), Paton (1999), Frahm and Frey (2004), Smith (2004), Frey et al. (2006), Atherton et al. (2010), and Lüth (2019). The species *Bryum pseudotriquetrum* and *B. bimum* are summarized as *B. pseudotriquetrum* aggr., since hardly any fertile samples were found. Conservation status of the species follows Schnyder et al. (2004) and Bornand et al. (2016).

A variety of structural and physico-chemical parameters were included as possible explanatory variables for species composition (Table 1). Water temperature at the outlet, water pH, water conductivity (as an indicator of mineral content, analogous to Sekulová et al. 2012), oxygen content, and oxygen saturation were measured at three locations per plot in open water. Signs of human or animal use were noted in the field and compared with federal and cantonal geodata (Federal Office of Topography swisstopo 2020; GeoGR 2020).

Structural survey

The structural surveys followed the method developed on behalf of the FOEN for the national inventory of spring habitats (Lubini et al. 2014; Küry et al. 2019) and the instructions for the structural surveys in the nature parks of Grisons (Küry 2018, unpublished). Several parameters from the structural records were included in the analysis (Table 1).

Table 1. Examined environmental parameters.

Parameter	Unit	Comment
Coordinates	°	World Geodetic System WGS 1984
Topography		
Elevation	m	Values extracted from the Swiss topographical model TLM25
Slope	°	
Maximum microrelief	cm	Perpendicular deviation of the surface from the plane
Hydrology		
Spring size	m²	Area of open water immediately around the spring outlet (Küry et al. 2019)
Discharge	l/s	Field approximation (Küry et al. 2019)
Maximum water depth	cm	
Vegetation		
Vegetation cover	%	Total vegetation; tree, shrub, herb, and cryptogam layers (shoot presence)
Canopy cover	%	App. % cover
Maximum height of herb layer	cm	
Substrate		
Coverage values	%	Open water, litter, dead wood, stones / rocks, gravel / coarse sand, fine soil
Carbonate content of soil	-	Ordinal scale (HCl test) (Bodenmann et al. 1997, modified)
Spring water		
Water temperature at outlet	°C	Multiprobe HQ40d (Hach)
Water conductivity	µS/cm	Multiprobe HQ40d (Hach)
Water pH	-	Multiprobe HQ40d (Hach)
Oxygen content	mg/l	Multiprobe HQ40d (Hach)
Oxygen saturation	%	Multiprobe HQ40d (Hach)

Classification

Unsupervised classification was performed using the modified TWINSPAN (Two Way Indicator Species Analysis) algorithm (Roleček et al. 2009) in the software JUICE (Tichý 2002) (v.7.1.25, 2020), with a minimum group size of 3 and the average Sørenson coefficient as similarity index. Pseudospecies cut levels of 0, 5, and 40% coverage were used to achieve the clearest possible diagnostic species for the groups and to optimize the spatial distribution of types in the ordination. Diagnostic species were determined based on the standardized phi coefficient (Chytrý et al. 2002; Tichý and Chytrý 2006), where phi values of 0.25 or greater were considered diagnostic, those equal to 0.5 or greater were considered highly diagnostic. Diagnostic species were tested for significance with Fisher's exact test (Fisher 1922). Species with a frequency greater than 50% in the corresponding type were defined as constant species. The resulting units were compared with syntaxa from the literature in order to classify them and characterize them ecologically. The dataset is not representative of all vegetation types in the region, nor of all spring types in Switzerland.

Statistical analysis

The data were managed using Vegedaz (Küchler 2019). Statistical analyses were performed in R (v.3.1.2, R Core Team 2017) within the RStudio environment (v.1.1.383, RStudio Team 2016). All alternative hypotheses were two-sided unless specifically stated. The significance level was set at $\alpha = 0.05$.

In Vegedaz, the square root-weighted means of ecological indicator values (EIV) for moisture, soil reaction, temperature, light, soil aeration, nutrient content (hereafter "nutrient EIV"), and humus content were calculated for each relevé (Landolt et al. 2010). In accordance with the Central Limit Theorem (Quinn and Keough 2002), verification of normal distribution was not required. If variances differed greatly (i.e., by a factor of 4), data were transformed using decadic logarithm or square root; if variances could not be brought within an acceptable range through transformation, significance of differences was tested using Welch's ANOVA (one-way), with Games-Howell tests for post-hoc analyses. Otherwise, the significance of differences in means was tested via one-way analysis of variance (ANOVA). Tukey tests were performed for the post-hoc analyses. In a few cases, Welch's *t*-test was used to determine the significance of differences between two independent groups.

Detrended correspondence analysis (DCA) was performed on the vegetation data using the R package "vegan" (v.2.5), with rare species downweighted (Oksanen et al. 2019). Indicator values and recorded environmental factors were passively projected onto a visualization of the ordination.

Results

Species richness

A total of 95 bryophytes and 164 vascular plant species were recorded. The mean species richness was 21.7 species in 1 m². The most species-rich plot was located on a large helocrene system used as summer pasture, characterized by 31 vascular plant and 10 bryophyte species in 1 m². The most common species were *Bryum pseudotriquetrum* aggr. (occurring in 70% of the relevés) and *Aster bellidiastrum* (62%). *Palustriella commutata* was recorded in about half of the plots, over both limestone and silicate. Seven species in the vegetation plots are endangered or potentially endangered in Switzerland, including *Tofieldia pusilla*, *Bryoerythrophyllum alpigenum* and *Catoscopium nigritum*.

Classification

Comparing different divisions, seven was the highest number of types for which each of the terminal groups yielded a well floristically defined unit of more than five relevés (Figure 3); this excludes Type 1, an outlier consisting of one relevé. For the assignment to higher syntaxa, types were grouped to best yield ecologically interpretable units. For most springs, all three relevés belonged to a common type; for six springs, the relevés were split across

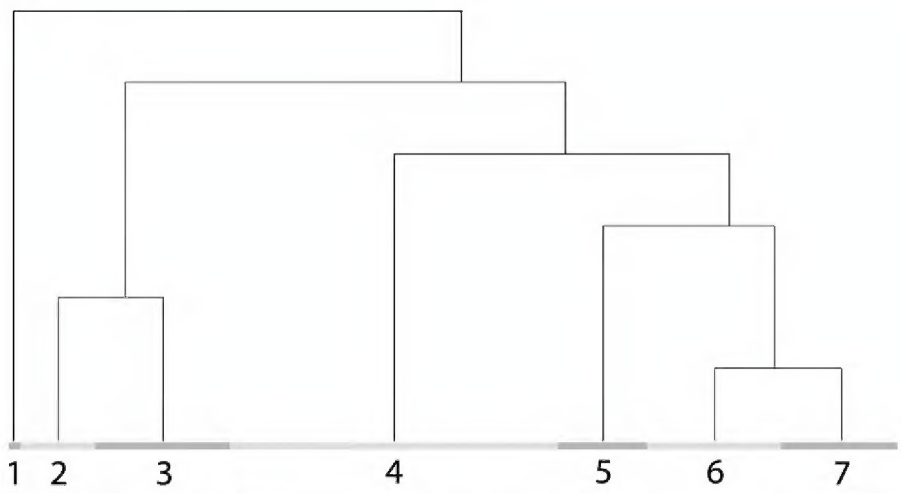

Figure 3. Dendrogram of the TWINSPAN-classification. The width of the bars is proportional to the number of vegetation plots included (one plot in case of cluster 1).

two types. Table 2 displays an abbreviated synoptic table (see Suppl. material 1 for full synoptic table and complete relevé table).

Comparison of vegetation types

Water pH differed little between vegetation types (mean 7.5–7.9) and oxygen content was mostly high (Suppl. material 3). Springs were mostly cold (water temperature at outlet 3.7–7.0°C) to slightly warm (7.0–11.0°C) (Suppl. material 3). The plots ranged from fully insolated to heavily shaded. The maximum height of the herb layer, often

Table 2. Abbreviated synoptic table from the numerical classification. Constancies are given as percentages; diagnostic (> 0.25) phi values are marked with (*), highly diagnostic (> 0.5) values with (**). Significant values are marked in light grey, highly significant values in dark grey. Diagnostic species (upper part of the table) passed Fisher's exact test, companion species did not pass the test. No diagnostic species are marked for Type 1 because it consists of a single relevé.

Type	**1**	**2**		**3**		**4**		**5**		**6**		**7**	
No. relevés	*1*	*5*		*9*		*21*		*5*		*6*		*13*	
Taxon													
Rhizomnium magnifolium	-	100	**	22		10		-		-		-	
Geranium sylvaticum	-	60	**	-		-		-		-		-	
Calamagrostis villosa	100	80	**	-		-		-		-		-	
Epilobium alsinifolium	-	20		78	**	-		-		-		-	
Saxifraga stellaris	-	-		67	**	14		-		-		-	
Brachythecium rivulare	-	80		100	*	14		20		-		15	
Chaerophyllum hirsutum	-	80		67	*	-		-		-		-	
Pinguicula alpina	-	-		-		71	**	-		-		-	
Selaginella selaginoides	-	-		-		67	**	-		-		15	
Salix foetida	-	-		-		52	**	-		-		-	
Palustriella falcata	-	20		-		52	**	-		-		-	
Arabis subcoriacea	-	-		22		52	**	-		-		-	
Juncus alpinoarticulatus	-	-		-		52	*	20		-		15	
Philonotis tomentella	-	-		22		43	*	-		-		-	
Fissidens dubius	-	-		-		5		80	**	-		15	
Platydictya jungermannioides	-	-		-		-		60	**	-		-	
Plagiochila asplenioides	-	-		-		-		80	**	33		8	
Knautia dipsacifolia	-	20		-		-		80	**	33		8	
Brachythecium glareosum	-	-		-		5		-		83	**	-	
Plagiomnium medium	-	-		-		-		-		50	**	-	
Carex davalliana	-	-		-		24		20		-		69	**
Cephalozia spec.	-	-		-		5		-		-		-	
Amblystegium serpens	-	-		-		-		-		-		8	
Agrostis stolonifera	-	-		56		5		40		-		38	
Alchemilla alpina aggr.	-	-		-		14		-		-		-	
Equisetum variegatum	-	-		11		43		-		-		31	
Aneura pinguis	-	-		33		57		20		67		46	
Aster bellidiastrum	-	40		33		76		100		67		54	
Anastrophyllum minutum	100	-		-		-		-		-		-	
Achillea millefolium aggr.	-	-		-		5		-		-		-	
Amblystegium tenax	-	20		11		-		-		-		-	
Amblystegium fluviatile	-	40		44		-		-		-		-	
Adenostyles alliariae	-	20		11		-		-		-		-	
Blindia acuta	-	-		-		29		-		-		-	
Alchemilla conjuncta aggr.	-	-		11		-		-		-		-	
Bartsia alpina	-	-		-		19		-		-		-	
Adenostyles alpina	-	-		-		5		-		33		-	
Alnus viridis	-	-		-		10		-		-		-	
Cephaloziella varians	-	-		11		-		-		-		-	
Carex sempervirens	-	-		-		14		-		-		-	
Angelica sylvestris	-	-		-		-		-		-		8	
Caltha palustris	-	20		-		5		-		-		15	
Briza media	-	-		-		-		-		-		8	
Brachypodium rupestre	-	-		-		-		20		-		8	
Aulacomnium palustre	-	-		11		-		-		-		-	
Avenella flexuosa	-	-		-		5		-		-		-	
Blepharostoma trichophyllum	100	20		-		5		-		-		-	
Calypogeia azurea	-	20		-		5		-		-		-	
Cardamine amara	-	-		-		-		-		-		15	

Table 3. Arithmetic mean, minimum, and maximum values of environmental variables over the entire survey. Significant differences are noted as follows: (***), highly significant ($p < 0.001$); (**), moderately significant ($0.001 \leq p < 0.01$); (*), significant ($0.01 \leq p < 0.05$); (n.s.), not significant. The ordinal scale of the carbonate content of the soil should be interpreted as follows: 0, no carbonate present; 1, only traces of carbonate; 2, < 2% carbonate; 3, 2–10% carbonate; 4, > 10% carbonate (Bodenmann et al. 1997, modified).

Topography	Mean	Min.	Max.	Test, Transformation	*p*-value	Significance
Elevation (m)	1,575	964	2,122	Welch's ANOVA	< 0.001	***
Slope (°)	19	4	46	ANOVA	0.911	n.s.
Maximum microrelief (cm)	22	4	77	ANOVA, log10	0.010	*
Hydrology						
Spring size (m²)	7	1	20	Welch's ANOVA	0.183	n.s.
Discharge (l/s)	5	0.03	25	Welch's ANOVA	0.005	**
Maximum water depth (cm)	5	0	26	ANOVA, log10	0.005	**
Vegetation						
Canopy cover (%)	28	0	82	ANOVA	0.415	n.s.
Maximum height of herb layer (cm)	54	16	150	ANOVA	0.559	n.s.
Coverage herb layer (%)	46	0.2	92	ANOVA	0.574	n.s.
Coverage moss layer (%)	50	5	96	Welch's ANOVA	0.503	n.s.
Species richness	21.7	10	41	ANOVA	0.845	***
Vascular plant species richness	13.6	5	31	Welch's ANOVA	< 0.001	
Bryophyte species richness	7.3	1	17	ANOVA	0.130	n.s.
Substrate						
Open water (%)	22	0	69	ANOVA	0.103	n.s.
Litter (%)	17	0.1	95	Welch's ANOVA	0.047	*
Dead wood (%)	3	0	20	Welch's ANOVA	0.792	n.s.
Stone, rock (%)	29	0	95	Welch's ANOVA	< 0.001	***
Gravel, coarse sand (%)	22	0	85	ANOVA	0.531	n.s.
Fine soil (%)	49	0	100	ANOVA	0.006	**
Carbonate content of soil	1.6	0	4	ANOVA	< 0.001	***
Spring water						
Water temperature at outlet (°C)	8.5	3.7	13.0	Welch's ANOVA	< 0.001	***
Water conductivity (µS/cm)	487	131	1299	Welch's ANOVA	< 0.001	***
Water pH	7.7	6.8	8.6	Welch's ANOVA	0.046	*
Oxygen content (mg/l)	7.37	0.17	10.81	Welch's ANOVA	< 0.001	***
Oxygen saturation (%)	78.7	1.9	108.6	Welch's ANOVA	< 0.001	***

measured on culms of *Deschampsia cespitosa*, averaged 54 cm. In the following passages, the types of the numerical classification are described and provisionally assigned to likely syntaxa. The full header data can be found in Suppl. material 2, characterization of the surveyed environmental parameters per vegetation type in Suppl. material 3. Boxplots of a selection of ecological parameters are displayed in Figure 4, while representative photos of each type are shown in Figure 5.

Type 1: strongly flowing rheocrene over boulders

This type consisted of a single plot in sparse mountain forest: a deep outlet of very cold water (3.8°C) under a massive rock overhang with mostly saxicolous vegetation. Many of the species present were unique in the survey (e.g. *Sphagnum capillifolium*, *Bryoerythrophyllum alpigenum*). In the ordination, this relevé lies more than 2 SD (standard deviation) away from its nearest neighbor (DCA axis 1). This type was excluded post-hoc from classification and final ordination for these reasons. The other relevés of this heterogeneous spring area belong to Types 2 and 3.

Type 2: Rhizomnium magnifolium-Chaerophyllum hirsutum community: mineral-poor springs in subalpine forest clearings

Diagnostic species: *Calamagrostis villosa*, *Geranium sylvaticum*, *Rhizomnium magnifolium*

This type was composed of many species that prefer sheltered sites. *Brachythecium rivulare* occurred frequently, while *Palustriella commutata* was absent. Litter cover was high, and the herb layer was vigorous (mean cover 58%, mean maximum height 88 cm). The spring water had low conductivity, was often oxygen-rich and very cold (mean water temperature at outlet 5.2°C). The type mostly consisted of rheocrenes with moderate to strong flow (mean discharge 6.2 l/s). The average maximum microrelief was 48.2 cm, significantly greater than in many other types (Figure 4D). Nutrient EIV was also significantly greater than in many other types (Figure 4G).

This type is difficult to classify. According to Hinterlang (1992) and Mucina et al. (2016), the *Cardamino-Chrysosplenietalia* Hinterlang 1992 always occurs below the spruce stage. The well-developed herb layer, predominance of shade-loving species, and strong flow suggest the *Caricion remotae* Kästner 1941 (Table 3). This alliance, although mostly associated with the montane zone, is also recorded at higher elevations (e.g., Grabherr and Mucina 1993; Chytrý 2011). Some traditional character species of the *Cardamino-Chrysosplenietum alternifolii* Maas 1959 are not present here, but that should not exclude the community: *Carex remota* does not grow above the montane level, and *Chrysosplenium alternifolium* rarely occurs in the area (Info Flora 2020). Some characteristic and dominant species of the community described by

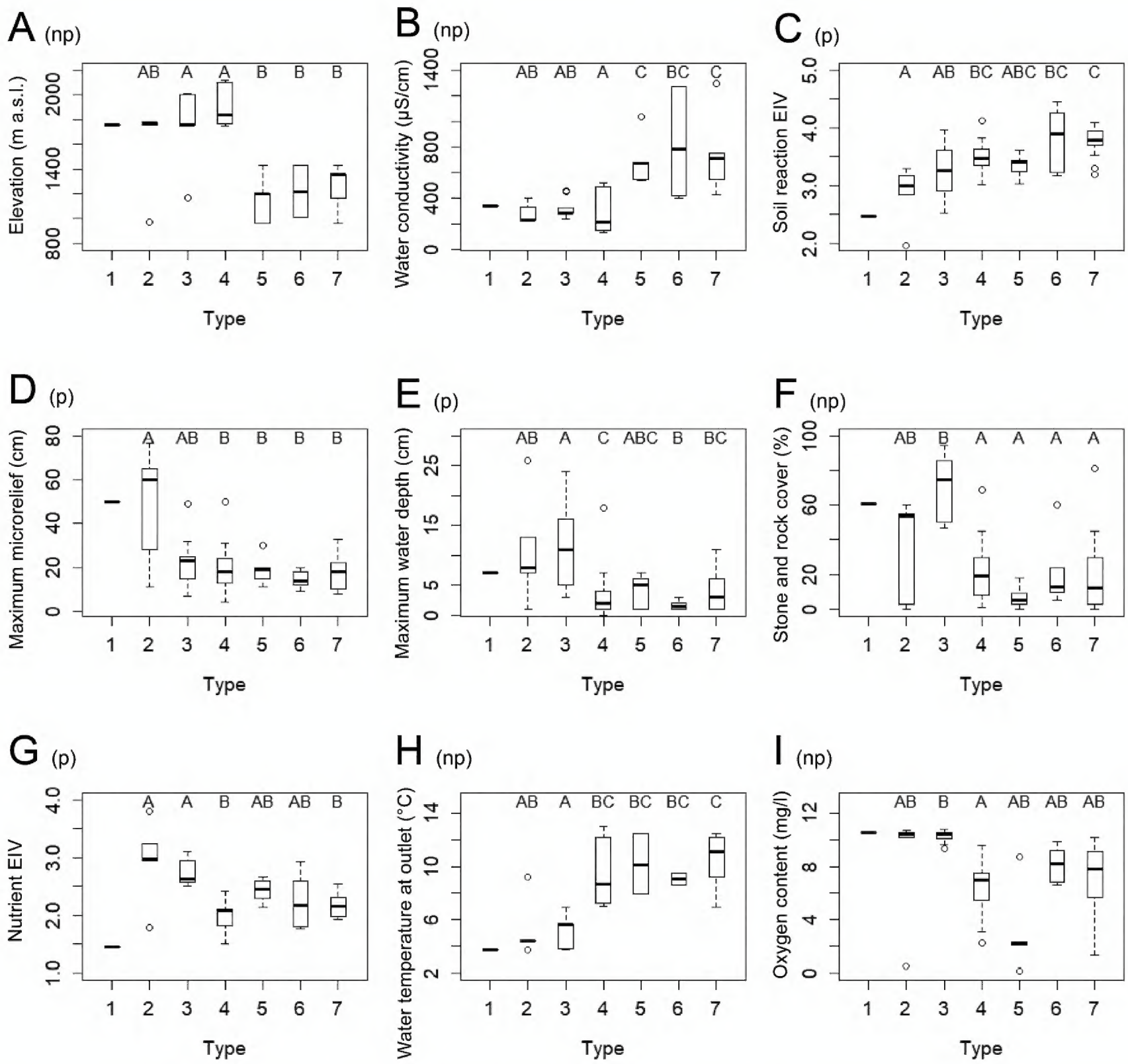

Figure 4. Boxplots of a selection of ecological parameters. Bars without common letters differ significantly from each other. Variables with (p) were assessed with parametric procedures (ANOVA, Tukey test), for variables with (np) non-parametric tests were used (Welch's ANOVA, Games-Howell test).

Chytrý (2011) are present (e.g. *Chaerophyllum hirsutum*, *Brachythecium rivulare*, *Conocephalum conicum*).

Type 3: Epilobium alsinifolium-Brachythecieum rivulare community: mineral-poor, cold-stenothermic, unshaded springs

Diagnostic species: *Brachythecium rivulare*, *Chaerophyllum hirsutum*, *Epilobium alsinifolium*, *Saxifraga stellaris*

This vegetation developed around rheocrenes of the subalpine zone under the influence of oxygen-rich, cold spring water (mean water temperature at outlet 5.1°C). Compared to other unshaded springs in the study, the water was significantly richer in oxygen (mean oxygen content 10.2 mg/l) (Figure 4I). The mean cover of the moss layer was comparatively high at 60%, and *Palustriella commutata* strongly dominated in many plots, which may explain the relatively low species richness. These relevés were mostly strongly flowing rheocrenes, with stone and rock cover exceeding many other types significantly (Figure 4F). Mosses dominated over vascular plants more strongly than in the other types.

This vegetation type shares a diagnostic species (*Epilobium alsinifolium*) with the *Cratoneuro-Philonotidetum seriatae* Geissler 1976. *E. alsinifolium* makes no special demands on substrate chemistry, but prefers very wet, cold sites (Geissler 1976; Oberdorfer 2001). The character species *Saxifraga stellaris* is also a cold-water specialist. Since there are certain similarities with the *Cratoneuro-Philonotidetum calcarae* Geissler 1976, the type may be an intermediate form between the two associations. Although the mean water conductivity of 319 µS/cm is high relative to other studies, Geissler gives 16 °dH (about 480 µS/cm) as the maximum value of total hardness for the association. The *Cratoneuro-Philonotidetum seriatae* is mostly found in the subalpine zone, where it is represented mainly by rheocrenes with considerable flow velocities. The *Brachythecium rivulare-Cardamine amara* variant described by Geissler (1976) includes stands along rapidly flowing headwater streams with strong stands of *Brachythecium rivulare*, as well as scattered occurrences of *Cardamine amara* and tall shrubs (e.g. *Petasites paradoxus* in this case).

Figure 5. Representative photographs of each vegetation type. **A** Type 2, mineral-poor springs in subalpine forest clearings; **B** Type 3, mineral-poor, cold-stenothermic, unshaded springs; **C** Type 4, mineral-poor springs in alpine pastures; **D** Type 5, mineral-rich, montane forest springs; **E** Type 6, mineral-rich forest springs; **F** Type 7, montane rich-fen springs. Photographs by Hallie Seiler (**A–E**) and Jürgen Dengler (**F**).

Type 4: Palustriella falcata-Pinguicula alpina community: mineral-poor springs in alpine pastures

Diagnostic species: *Arabis subcoriacea*, *Juncus alpinoarticulatus*, *Palustriella falcata*, *Philonotis tomentella*, *Pinguicula alpina*, *Salix foetida*, *Selaginella selaginoides*

These relevés included oligotrophic springs on pastures in the subalpine to alpine zones. The plots were evenly divided between rheo- and helocrenes. The most species-rich relevés in the survey belonged to this type (mean 24.3 species in 1 m^2). These springs were mostly fully insolated or were only lightly shaded. In some cases, very high water temperatures were recorded in shallow pools. Water was significantly shallower than in Types 2 and 3 (Figure 4E). The nutrient EIV was significantly lower than the other high elevation springs (Figure 4G).

The records of this type are similar to *Philonoto fontanae-Montietum rivularis* Büker et Tx. 1941. This community is found in moderately warm alpine springs over siliceous bedrock and is associated with grazing. The character species *Philonotis tomentella* is also diagnostic here, and the calcifuge *Diobelonella palustris* occurs sporadically. Compared to *Pinguicula vulgaris*, the diagnostic species *P. alpina* is more likely to occur in high mountains and is less bound to limestone (Oberdorfer 2001). However, it is questionable whether this vegetation type could be assigned to a siliceous alliance: although the substrate is carbonate-poor,

many typical species of the *Cratoneurion* are present, including the character species *Pinguicula alpina* and *Palustriella falcata*, which are diagnostic for this type. One possible solution would be to understand the alliance *Cratoneurion* as a collection of subalpine-alpine spring communities over both limestone and silicate, as proposed by Geissler (1976). The *Cratoneuro-Philonotidetum calcareae* Geissler 1976 appears to be a suitable match. Diverse calcicoles are present, and the differential species *Arabis subcoriacea* is diagnostic and common. This species colonizes base-rich, humic soils as well as weakly trickling springs over gravel (Oberdorfer 2001). *Brachythecium rivulare* is conspicuously rare, and *Saxifraga aizoides* is more common than *S. stellaris*, as is characteristic for the association.

Type 5: Fissidens dubius-Cratoneuron decipiens community: mineral-rich, montane forest springs

Diagnostic species: *Fissidens dubius*, *Knautia dipsacifolia*, *Plagiochila asplenioides*, *Platydictya jungermannioides*

These helocrenes were found in forests of the montane zone. The substrate was basic (soil reaction EIV), nutrient-rich (nutrient EIV), and fine. The oxygen content of the spring water was significantly lower than many other types (mean 3.1 mg/l) (Figure 4I). Canopy cover varied widely. Relevés included springs with severe trampling damage from wildlife. Springs tended to be small and weakly flowing (mean discharge 0.2 l/s). Herb layer cover was mostly higher than that of the moss layer, which is unusual for this study.

The alliance *Lycopodo europaei-Cratoneurion commutati* Hadač 1983 could be considered here. These calcareous forest springs, although mostly associated with the colline and montane zones, occur almost to the timberline according to Chytrý (2011), and have been recorded in the Italian Alps (Giacomini 1939, assigned by Dierssen 1973). The only association of the alliance, *Brachythecio rivularis-Cratoneuretum* Dierssen 1973, has a similar ecomorphology and species assemblage (e.g., *Palustriella commutata* (diagnostic), *Eucladium verticillatum* (diagnostic) and *Equisetum palustre* (dominant)). According to Hájek (1998), this community occurs in both heavily and lightly shaded habitats. Tufa does not occur in the relevés, probably due to local climatic conditions, although microscopic carbonate crystals were observed in many bryophyte samples. For three springs, assignments were split across Types 5 and 7, presumably due to varying light conditions in the spring area.

Type 6: Plagiomnium medium-Palustriella commutata community: mineral-rich forest springs

Diagnostic species: *Brachythecium glareosum*, *Plagiomnium medium*

These records were superficially similar to Type 5: they were also base-rich, shaded springs of the montane stage. The springs were either rheocrenes or linear springs. Half of the relevés were tufaceous, and the relevés were species-poor on average (mean 18.3 species in 1 m^2). Water was better oxygenated in contrast to type 5 (Figure 4I), and nutrient EIVs were low. These large springs occurred on steep, wooded slopes.

The relevés of this type belong to two forest springs with very different environmental conditions: a linear spring without tufa formation and a very large, complex rheocrene system with cascade tufa. The question arises as to why they were combined in the classification. There are only a few species that can persist under strong tufa formation; however, these can often occur on other base-rich, wet sites, so they are usually not strictly tied to petrifying springs (Zemp et al. 2016). The rarity of true character species for petrifying springs leads to them being distributed here over two types (6 and 7). Lyons and Kelly (2017) note that the definition of *Cratoneurion* vegetation has long been problematic, and that transitions between petrifying springs and other habitats are poorly characterized, although widely recognized in the literature. The linear forest spring could probably be assigned to the *Brachythecio rivularis-Cratoneuretum*, while the large tufaceous spring potentially belongs to the *Eucladietum verticillati* Allorge 1922. This community occurs on steep, wet limestone rock faces, often in partial shade (Grabherr and Mucina 1993). Grabherr and Mucina (1993) found the second association at elevations up to 1,500 m in Austria, although the community has otherwise rarely been recorded there. The character species *Eucladium verticillatum* is present, but not dominant, as indicated in the literature. Otherwise, many of the numerous companion species of the association are present: *Tofieldia calyculata*, *Carex flacca*, *Palustriella commutata*, and *Agrostis stolonifera*. *Catoscopium nigritum*, a pioneer species of tufa cascades (Schubert et al. 2001), was found in one plot. Although tufaceous springs also belong to Type 7, those formations consist of terraces rather than slabs.

Type 7: Carex davalliana-Palustriella commutata community: montane rich fen-springs

Diagnostic species: *Carex davalliana*

This vegetation type was influenced by warm, base-rich spring water, sometimes with tufa formation. With the exception of one plot, this type was located in helocrenes (69%) or linear springs. Canopy cover varied from 14 to 68%, but species mostly had moderately high light EIVs (mean 3.34). The water temperatures at the outlet were significantly higher than in Type 3 (Figure 4H). The fine, calcareous substrate was rather weakly percolated.

This type shares many species with rich fens, including *Carex davalliana* (diagnostic), *Carex lepidocarpa* (constant), and *Tofieldia calyculata*. However, character species of the *Cratoneurion* (*Palustriella commutata* and *Aneura pinguis*) occur frequently, and *Hymenostylium recurvirostrum* (character species) and *Pinguicula vulgaris* (companion species) are also present. The *Cratoneuretum commutati* Aichinger 1913 could be considered: this vegetation occurs in calcareous springs of the montane stage and possesses the character species *Cratoneuron filicinum* aggr., present in the relevés, a rather nitrophilous species that tolerates desiccation better than *Palustriella commutata* (Lyons and Kelly 2017).

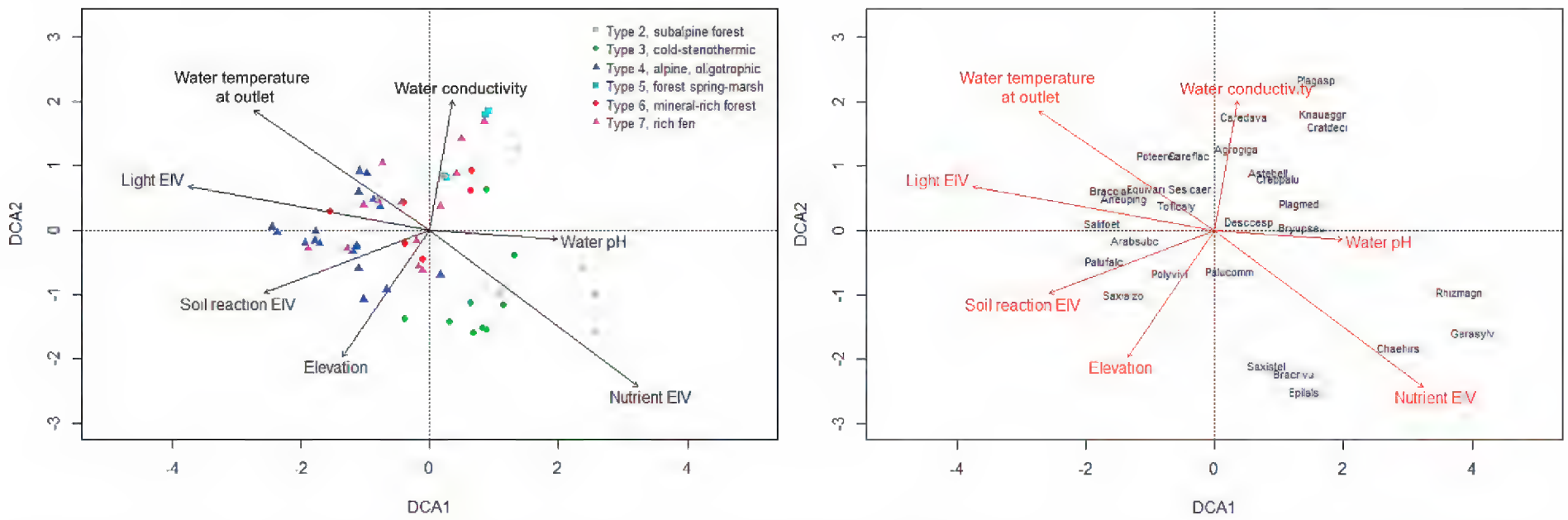

Figure 6. Gradient analysis (DCA) of the dataset. Environmental variables and EIVs are projected over the ordination. The vectors shown correlate with at least |*r*| = 0.80 with one of the two axes. Above – vegetation types; below – the 20 most common species in the relevés, as well as the diagnostic species of the numerical classification, are shown: "Arabsubc" – *Arabis subcoriacea*; "Agrogiga" – *Agrostis gigantea*; "Aneuping" – *Aneura pinguis*; "Astebell" – *Aster bellidiastrum*; "Bracglar" – *Brachythecium glareosum*; "Bracrivu" – *Brachythecium rivulare*; "Bryupseu" – *Bryum pseudotriquetrum* aggr.; "Caredava" – *Carex davalliana*; "Careflac" – *Carex flacca*; "Chaehirs" – *Chaerophyllum hirsutum*; "Cratdeci" – *Cratoneuron decipiens*; "Desccesp" – *Deschampsia cespitosa*; "Epilalsi" – *Epilobium alsinifolium*; "Equivari" – *Equisetum variegatum*: "Gerasylv" – *Geranium sylvaticum*; "Knauaggr" – *Knautia dipsacifolia*; "Palufalc" – *Palustriella falcata*; "Palucomm" – *Palustriella commutata*; "Plagaspl" – *Plagiochila asplenioides*; "Plagmedi" – *Plagiomnium medium*; "Polyvivi" – *Polygonum viviparum*; "Poteerec" – *Potentilla erecta*; "Rhizmagn" – *Rhizomnium magnifolium*; "Salifoet" – *Salix foetida*; "Saxiaizo" – *Saxifraga aizoides*; "Seslcaer" – *Sesleria caerulea*; "Toficaly"– *Tofieldia calyculata*.

The frequent interlocking with the *Caricion davallianae* is also mentioned in the literature (Knapp and Stoffers 1962; Grabherr and Mucina 1993); indeed, some plots of this type might be better assigned to that alliance. This type includes spring sites whose relevés were sometimes assigned to Types 2 and 3 (both mineral-poor types of the subalpine zone), underscoring the difficulty of differentiating spring vegetation on the basis of water chemistry.

Environmental gradients

DCA axes 1 and 2 explain much of the variation in species composition (eigenvalues 0.66 and 0.54, respectively, Figure 6). The length of axis 1 is 5.09 standard deviations (SD), signaling high β-diversity, so the two ends of the gradient share few common species. Axis 2 has gradient length 3.51, justifying the use of DCA. DCA axis 1 correlates most strongly with water pH (|*r*| = 0.998), light EIV (|*r*| = 0.984), soil reaction EIV (|*r*| = 0.935), and nutrient EIV (|*r*| = 0.799), while DCA axis 2 correlates most strongly with water conductivity (|*r*| = 0.984) and elevation (|*r*| = 0.825). Vegetation Type 1 (*n* = 1) was omitted from the ordination.

Discussion

Species richness

The species richness of the records (95 moss species, 164 vascular plant species) is high compared to similar studies. In Gesäuse National Park (AT), 97 vascular plants and 60 bryophyte species were recorded in 46 plots of less than 1 m² (Suanjak 2007). Mogna et al. (2015) found 135 species of bryophytes and vascular plants in 48 springs in the Ligurian Alps (Italy). In the Kalkalpen (Austria), Weigand (1998) recorded 77 bryophyte species in 22 springs. In a study of 19 springs in the Adamello-Brenta Regional Park (Italy), Cantonati and Ortler (1998) found only 58 bryophyte species, but an astonishing 245 vascular plant species. For springs in the Swiss Alps, western Carpathians, and mountains of Bulgaria, Sekulová et al. (2012) found a mean species richness of 25.0, 22.2, and 17.3 species in 16 m², respectively. The GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019) gives a mean total species count of 15.4 species in 1 m² (*n* = 493) for wetlands in alpine, boreal, and temperate climates (GrassPlot Diversity Explorer v. 2.10; https://edgg.org/databases/GrasslandDiversityExplorer; see Biurrun et al. 2021); in this study, a mean species count of 21.7 species in 1 m² was recorded. However, few records of *Montio-Cardaminetea* are represented in the database at present, and other wetlands (e.g., reedbeds and riparian habitats) are generally species-poorer on average. It is unclear why the records in Parc Ela were so species rich, especially when the species-area relationship is considered (Chytrý and Otýpková 2003). One possible explanation is the inclusion of springs with widely varying environmental conditions.

Site conditions

The ecological conditions of springs are generally difficult to assess because they are small habitats characterized by strong ecotones (Brunke et al. 2015). For this study, only

a single measurement of the physico-chemical parameters was made, although Cantonati et al. (2006) recommend that these parameters be recorded over at least one year. Although spring water generally undergoes only minor physico-chemical changes during the course of a year (Odum 1971), it is unknown how parameters vary seasonally within the study area. The FOEN method (Küry et al. 2019) is practical for rapid survey of key characteristics, but many parameters are rough estimates.

Vegetation types are clearly separated by elevation and water conductivity (Figure 4A and 4B). The first group (Types 1 to 4) includes springs of the subalpine-alpine levels with a mean water conductivity around 297 µS/cm (SD = 126 µS/cm). The moderately low conductivity could be related to the geology of the aquifer and/or short groundwater residence time (Catonati and Ortler 1998). The mean soil reaction EIV corresponds to a pH between weakly acidic and neutral (mean 3.31, SD = 0.43). The second group consists of montane springs with higher water conductivities (mean 748 µS/cm, extreme values up to 1,299 µS/cm). Here, according to the soil reaction EIV, the substrate is somewhat more base-rich than in the first group (mean 3.68, SD = 0.37). The differences within mean elevation and water conductivity are statistically significant ($p < 0.001$ and $p = 0.002$, Welch's t-test, one-sided). The average temperature EIV of the second group is significantly higher ($p = 0.018$, Welch's t-test, one-sided), but the difference in means is not large (mean group 1 = 2.27, group 2 = 2.60).

There is an apparent gradient of shading within the main groups, but it is not statistically significant in the overall data set, although it explains much of the variability in the ordination (light EIV, $|r| = 0.984$ with DCA axis 1).

Classification and syntaxonomy

This study was affected by the oft-cited paucity of diagnostic species particular to spring habitats (Oberdorfer 1992; Beierkuhnlein and Gollan 1999). Of the 21 diagnostic species calculated, less than half belong to the classic character species for syntaxa of the *Montio-Cardaminetea*. However, this is presumably related to methodological limitations: since only spring vegetation data were included, many of the diagnostic species are probably differential species that are more common in other habitats.

Epilobium alsinifolium, listed as a class character species of *Montio-Cardaminetea*, appears in these records only in the Types 2 and 3, presumably due to temperature-related effects. The class character species *Stellaria alsine* and *Bryum schleicheri* (Schubert et al. 2001) do not occur in the records; *Stellaria alsine* is a calcifuge forest species which does not occur in the region. According to Oberdorfer (2001), *Cardamine amara* prefers humic, nutrient-rich sites, and occurs only sporadically in springs; in this study, it was encountered in only three relevés. In addition, Pott (1995) notes that the species transgresses too much into reedbeds and alder carrs to be a strong character species of the class.

Although the water conductivity was mostly not very low (Figure 4), species of the *Cardamino-Montion* did occur. The alliance character species *Diobelonella palustris* was observed sporadically, but the main distributional range of *Montia* spp. ceases north of the Alps (Hinterlang 2017) and the genus, like the alliance character species *Epilobium obscurum*, is rare in the mountains of Switzerland (Info Flora 2020). Other differential species of the alliance, *Calliergonella cuspidata* and *Juncus articulatus* (Hinterlang 2017), occur as well, but are not strictly tied to siliceous substrate (Oberdorfer 2001; Atherton et al. 2010). The species assemblage of the unshaded springs mostly agrees with the classic *Cratoneurion commutati*; the problem is rather that the typical species of the alliance (e.g. *Palustriella commutata*, *Saxifraga aizoides*) are also quite common over siliceous bedrock in the Alps.

The delimitation between spring and contact community is challenging, which complicates the selection of areas for vegetation surveys: in the literature, very different area sizes are recorded, between 0.04 to 80 m² (Chytrý and Otýpková 2003; see also Pott 1995). Fragmentary or weakly developed stands are often ignored in favor of homogeneous small-scale sites (Cantonati et al. 2006), which was not done in this study; therefore, comparisons with existing syntaxa should be viewed critically.

The numerical classification results in seven vegetation types which seem to occupy a rank between alliance and association. For this classification, the forest springs were neither simply split off into a separate alliance, nor were they merged with unshaded springs of similar chemistry. Although some researchers (e.g., Delarze et al. 2015) treat forest spring synusia as components of forest communities, we share the view of Kästner (1941). The vegetation of forest springs, although dependent on shading, has characteristic species compositions which have been attested by numerous authors as separate types (e.g. Braun-Blanquet 1926; Tüxen 1937; Maas 1959; Hinterlang 1992).

The description and comparison of types results in the proposed syntaxonomy in Table 4. All unshaded communities can be assigned to the *Cratoneurion*, a TypoCH-alliance which is listed in the Ordinance on the Protection of Nature and Cultural Heritage as "deserving of protection." These communities can be provisionally divided into two "suballiances" of the *Cratoneurion*: a montane group, and a group sensu Geissler (1976), which includes subalpine-alpine springs over calcareous and siliceous bedrock. The position of the alliances is controversial. Mucina et al. (2016) place the *Caricion remotae* within a separate order (*Cardamino-Chrysosplenietalia* Hinterlang 1992) and note that the *Cratoneurion* may better be placed in the *Adiantetea* Br.-Bl. et al. 1952. Additionally, they suggest reducing the *Lycopodo-Cratoneurion* to a synonym of the *Cratoneurion*. This may be justified in our case, since no clear separation between shaded and unshaded springs over limestone could be shown.

Table 4. Proposed syntaxonomy for the studied spring sites.

***Montio-Cardaminetea* Br.-Bl. et Tüxen ex Klika et Hadač 1944**
- ***Montio-Cardaminetalia* Pawłowski et al. 1928**
  - ***Cratoneurion commutati* Koch 1928**
    - **Montane associations**
      - ° *Eucladietum verticillati* Allorge 1922
      - ° *Cratoneuretum commutati* Aichinger 1913
    - **Subalpine-alpine associations**
      - ° *Cratoneuro-Philonotidetum calcareae* Geissler 1976
      - ° *Cratoneuro-Philonotidetum seriatae* Geissler 1976
  - ***Lycopodo europaei-Cratoneurion commutati* Hadač 1983**
    - ° *Brachythecio rivularis-Cratoneuretum* Dierssen 1973
- ***Cardamino-Chrysosplenietalia* Hinterlang 1992**
  - ***Caricion remotae* Kästner 1941**
    - ° *Cardamino-Chrysosplenietum alternifolii* Maas 1959

Environmental gradients

The two visualized DCA axes show high heterogeneity along their lengths. DCA axis 1 can be interpreted as a gradient from highly insolated, oligotrophic springs to somewhat more nutrient-rich forest springs with base-rich water (Figure 6). Nutrient EIV increases with increasing shading, possibly due to the allochthonous input of organic material. Temperature EIV also increases slightly in association with this gradient, as shaded springs are better sheltered from cold and usually occur below the timberline. As the axis value increases, typical species of forests and tall forb communities occur (e.g. *Geranium sylvaticum*, *Chaerophyllum hirsutum*). At the lower end of the axis, species of the subalpine-alpine unshaded springs are more likely to be found, such as *Palustriella falcata* and *Saxifraga aizoides*. DCA axis 2 is most strongly correlated with water conductivity and elevation. In the lowest range of values are the species of cold springs, such as *Saxifraga stellaris* and *Epilobium alsinifolium*. *Carex davalliana*, as a calcicole, lies in the highest range of the axis.

In the ordination it can be clearly seen that elevation is a sum parameter which integrates diverse factors and catchment processes (Strohbach et al. 2009). As elevation increases, the mineral content of the spring water decreases and the mean annual temperature decreases. Habitats become more strongly insolated and nutrient-poor. However, no strong pattern is evident in the ordination with respect to soil reaction, despite high correlation with DCA axis 1. The intermingling of calcifuges and calciphiles in the ordination is consistent with the observed reality in the field. As in other studies (e.g., Beierkuhnlein and Gräsle 1998; Hájek et al. 2002; Hájkova et al. 2008), water pH was found to be an important parameter for species composition, although the effect is likely obscured by the discrepancy between spring water chemistry and substrate chemistry at the sites.

Implications for conservation efforts

The ordination confirms that nutrient EIV is an important factor for species composition ($|r| = 0.799$ with DCA axis 1). Since eutrophication quickly leads to the depletion of specialized bryophytes in oligotrophic wetlands (Bergamini and Pauli 2001; Hedenäs et al. 2003), local farmers in Parc Ela carry particular responsibility for these sites. Interestingly, the most species-rich areas in the study were on low-intensity grazed pastures; however, it is possible that highly specialized spring species are adversely affected by this disturbance. Trampling by game or livestock was observed in 20% of the relevés in this study, with the most severely damaged springs located in montane forests. Helocrenes were observed to be impacted by forest management, through trampling and inputs of forest debris during timber harvesting. Zollhöfer (1997) reports that such springs also fall victim to logging trails. For this reason, we consider it necessary to involve forestry operations in conservation projects.

Parc Ela has a good ecological infrastructure which is continuously being reinforced. Spring restoration projects, rare in Switzerland to date, likely have a good chance of success within the park; however, Cantonati et al. (2006) note that research is needed to understand how typical spring flora can be effectively restored, if at all. This survey was limited to relatively natural springs of the montane and subalpine levels, providing basic knowledge on the ecological potential of many local springs. For further development of a protection concept, comparable studies for impaired springs or those near settlements are recommended.

Outlook

This study confirms the oft-cited species richness of spring habitats. For the protection of these valuable habitats, many new developments can be expected in the coming years, such as the planned European revision of the class *Montio-Cardaminetea* (cf. Hájek et al., pers. comm.) and completion of the national inventory of spring habitats in Switzerland. However, regional projects remain important. Since many species of bryophytes are highly specialized to springs (Cantonati et al. 2006), they should be used for monitoring and evaluations of the effectiveness of conservation measures.

In the future, a refined typology must be considered for spring conservation. This study identifies three major challenges to typifying the montane-subalpine springs of the central Alps: the complex geological and topographical conditions prevent simple division by groundwater chemistry; petrifying springs are floristically hardly distinguishable from other base-rich springs (and definition based on tufa formation is unsatisfactory; Lyons and Kelly 2017); and subalpine forest springs, although clearly distinguishable, are not taken into account in the existing Swiss classification system. These points should be considered for future conservation efforts.

Although the network of spring habitats is more intact in the high mountains than in the lowlands, many threats still exist. In this study, the importance of nutrient balance for plant species composition is confirmed; however, for the numerous oligotrophic springs on alpine pastures,

the extent of the ecological influence of this type of land use is still unclear. Climatic conditions may also become problematic in the coming years: because high-elevation springs depend on catchment snowpack and glaciers (Brown et al. 2003; Hannah et al. 2007), these disjunct habitats and their communities will react strongly to climate change (Woodward et al. 2010; Küry et al. 2018). Further studies of alpine springs, including long-term monitoring, could provide important information.

As the "water castle of Europe," Switzerland bears a strong responsibility to preserve its natural springs. Although there are many challenges facing spring conservation, renewed national scientific interest should do much to protect these valuable habitats.

Data availability

The data are provided as supplementary material and also included in the GrassPlot database (https://edgg.org/databases/GrassPlot).

Author contributions

The project was planned jointly by H.S., J.D., and D.K.; H.S. carried out the field sampling and plant determination with support from J.D. and D.K.; H.S. performed the analyses and drafted the manuscript under the guidance of J.D.; all authors checked, improved, and approved the manuscript.

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References

Atherton I, Bosanquet SDS, Lawley M (2010) Mosses and liverworts of Britain and Ireland: A field guide. British Bryological Society, London, UK, 848 pp.

Audorff V, Kapfer J, Beierkuhnlein C (2011) The role of hydrological and spatial factors for the vegetation of Central European springs. Journal of Limnology 70: 9–22. https://doi.org/10.4081/jlimnol.2011.s1.9

Beierkuhnlein C, Gollan T (1999) Ökologie silikatischer Waldquellen in Mitteleuropa. Bayreuther Forum Ökologie 71: 1–256.

Beierkuhnlein C, Gräsle W (1998) The influence of light regime and water chemistry on the structure of forest spring vegetation. In: Botosaneanu L (Ed.) Studies in crenobiology: the biology of springs and springbrooks. Backhuys, Leiden, NL, 9–22.

Berg C, Dengler J, Abdank A, Isermann M [Eds] (2004) Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Textband. Weissdorn, Jena, DE, 606 pp.

Bergamini A, Pauli D (2001) Effects of increased nutrient supply on bryophytes in montane calcareous fens. Journal of Bryology 23: 331–339. https://doi.org/10.1179/jbr.2001.23.4.331

Biurrun I, Burrascano S, Dembicz I, Guarino R, Kapfer J, Pielech R, García-Mijangos I, Wagner V, Palpurina S, …, Dengler J (2019) GrassPlot v. 2.00 – first update on the database of multi-scale plant diversity in Palaearctic grasslands. Palaearctic Grasslands 44: 26–47. https://doi.org/10.21570/EDGG.PG.44.26-47

Biurrun I, Pielech R, Dembicz I, Gillet F, Kozub Ł, Marcenò C, Reitalu T, Van Meerbeek K, Guraino R, …, Dengler J (2021) Benchmarking plant diversity of Palaearctic grasslands and other open habitats. Journal of Vegetation Science 32: e13050. https://doi.org/10.1111/jvs.13050

Bodenmann M, Siegenthaler A, Brunner J (1997) Kartieren und Beurteilen von Landwirtschaftsböden: Kartieranleitung. Eidg. Forschungsanstalt für Agrarökologie und Landbau FAL, Zurich, CH, 175 pp.

Bornand C, Gygax A, Juillerat P, Jutzi M, Möhl A, Rometsch S, Sager L, Santiago H, Eggenberg S (2016) Rote Liste Gefässpflanzen. Gefährdete Arten der Schweiz. Umwelt-Vollzug Nr. 1621. Federal Office of the Environment FOEN, Bern and Info Flora, Geneva, CH, 178 pp.

Braun-Blanquet J (1926) Ètudes phytosociologiques en Auvergne. Arvernia 2: 29–48.

Braun-Blanquet J (1949) Übersicht der Pflanzengesellschaften Rätiens (III). Vegetatio 1: 285–316. https://doi.org/10.1007/BF00184536

Brown LE, Hannah DM, Milner AM (2003) Alpine stream habitat classification: an alternative approach incorporating the role of dynamic water spring contributions. Arctic, Antarctic, and Alpine Research 35: 313–322. https://doi.org/10.1657/1523-0430(2003)035[0313:ASHCAA]2.0.CO;2

Brunke M, Hahn HJ, Martin P, Brendelberger H (2015) Grundwassergeprägte Lebensräume: eine Übersicht über Grundwasser, Quellen, das hyporheische Interstitial und weitere grundwassergeprägte Habitate. Limnologie Aktuell 14: 1–266.

Burck O (1947) Die Laubmoose Mitteleuropas. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft 477: 1–198.

Cantonati M, Ortler K (1998) Using spring biota of pristine mountain areas for long term monitoring: hydrology, water resources and ecology in headwaters. Proceedings of the International Association of Hydrological Sciences 248: 379–385.

Cantonati M, Gerecke R, Bertuzzi E (2006) Springs of the Alps – sensitive ecosystems to environmental change: from biodiversity assessments to long-term studies. Hydrobiologia 562: 59–96. https://doi.org/10.1007/s10750-005-1806-9

Chytrý M [Ed.] (2011) Vegetation of the Czech Republic – 3. Aquatic and wetland vegetation. Academia, Prague, CZ, 580–609.

Chytrý M, Otýpková Z (2003) Plot sizes used for phytosociological sampling of European vegetation. Journal of Vegetation Science 14: 563–570. https://doi.org/10.1111/j.1654-1103.2003.tb02183.x

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Delarze R, Gonseth Y, Eggenberg S, Vust M (2015) Lebensräume der Schweiz: Ökologie – Gefährdung – Kennarten. 3rd edn. Hep Verlag, Bern, CH, 456 pp.

Delarze R, Eggenberg S, Steiger P, Bergamini A, Fivaz F, Gonseth Y (2016) Rote Liste der Lebensräume der Schweiz: Aktualisierte Kurzfassung zum technischen Bericht 2013. Federal Office of the Environment FOEN, Bern, CH, 34 pp.

Dengler J (2003) Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. Archiv naturwissenschaftlicher Dissertationen 14: 1–297.

Dengler J, Berg C, Jansen F (2005) New ideas for phytosociological monographs. Annali di Botanica, Nuova Serie 5: 193–210.

Dengler J, Löbel S, Dolnik C (2009) Species constancy depends on plot size – a problem for vegetation classification and how it can be solved. Journal of Vegetation Science 20: 754–766. https://doi.org/10.1111/j.1654-1103.2009.01073.x

Dengler J, Wagner V, Dembicz I, García-Mijangos I, Naqinezhad A, Boch S, Chiarucci A, Conradi T, Filibeck G, …, Biurrun I (2018) GrassPlot – a database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48: 331–347. https://doi.org/10.1127/phyto/2018/0267

Dierssen K (1973) Die Cratoneurum-Gesellschaft einiger Quellbäche in den Bückebergen bei Bad Eilsen. Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft 15–16: 22–27.

Eggenberg S, Möhl A (2013) Flora vegetativa: Ein Bestimmungsbuch für Pflanzen der Schweiz im blütenlosen Zustand. 3rd edn. Haupt, Bern, CH, 733 pp.

Ellenberg H, Klötzli F (1972) Wadgesellschaften und Waldstandorte der Schweiz. Mitteilungen der schweizerischen Anstalt für das forstliche Versuchswesen 48(4): 589–930.

Federal Office of Meteorology and Climatology MeteoSwiss (2020) Climate diagrams and normal per station. https://www.meteoswiss.admin.ch/home/climate/swiss-climate-in-detail/climate-normals/climate-diagrams-and-normals--per-station.html [accessed 2 Dec 2020].

Federal Office of Topography swisstopo (2020) Geological and nature conservation maps. https://map.geo.admin.ch [accessed 2 Dec 2020]

Fisher RA (1922) On the interpretation of χ^2 from contingency tables, and the calculation of P. Journal of the Royal Statistical Society 85(1): 87–94. https://doi.org/10.2307/2340521

Frahm J-P, Frey W (2004) Moosflora. 4th edn. Ulmer, Stuttgart, DE, 538 pp.

Frey W, Frahm J-P, Fischer E, Lobin W (2006) Liverworts, mosses and ferns of Europe. Harley Books, Colchester, UK, 512 pp. https://doi.org/10.1163/9789004475434

Geissler P (1976) Zur Vegetation alpiner Fliessgewässer: Pflanzensoziologisch-ökologische Untersuchungen hygrophiler Moosgesellschaften in den östlichen Schweizer Alpen. Beiträge zur Kryptogamenflora der Schweiz 14: 1–55.

GeoGR (2020) Maps of biotopes, landscapes, wildlife and agricultural land use. https://geogr.mapplus.ch/viewer/ [accessed 11 Oct 2020]

Giacomini V (1939) Studi briogeographici. I. Associazioni di Briofite in Alta Valcamonica e in Valfurva (Alpi Retiche di Lombardia) [Biogeographical study. I. Bryophyte associations in Alta Valcamonica and Valfurva (Rhaetian Alps of Lombardy)]. Atti dell'Istituto Botanico "Giovanni Briosi" e Laboratorio Crittogamica Italiano della Reale Università di Pavia, Ser. 4, 12: 1–139.

Grabherr G, Mucina L [Eds] (1993) Die Pflanzengesellschaften Österreichs – Teil 2: Natürliche waldfreie Vegetation. 1st edn. Gustav Fischer, Jena, DE, 552 pp.

Hájek M (1998) Mokřadní vegetace Bílých Karpat [Wetland vegetation of the White Carpathians]. 1st edn. Sborník Přírodovědného klubu v Uherském Hradišti, Uherské Hradiště, CZ, 158 pp.

Hájek M, Hekera P, Hájková P (2002) Spring fen vegetation and water chemistry in the western Carpathian flysch zone. Folia Geobotanica 37: 364–364. https://doi.org/10.1007/BF02805220

Hájková P, Hájek M, Apostolova I, Zelený D, Dítě D (2008) Shifts in ecological behaviour of plant species between two distant regions: evidence from the base richness gradient in mires. Journal of Biogeography 35: 282–294.

Hannah DM, Brown LE, Milner AM, Gurnell AM, McGregor GR, Petts GE, Smith BP, Snook DL (2007) Integrating climate–hydrology–ecology for alpine river systems. Aquatic Conservation 17: 636–656. https://doi.org/10.1002/aqc.800

Hedenäs L, Bisang I, Schnyder N (2003) The distribution of bryophytes in Switzerland and Liechtenstein. IV. *Hamatocaulis* and *Pseudocalliergon*. Botanica Helvetica 113: 111–123.

Heino J, Virtanen R, Vuori K-M, Saastamoinen J, Ohtonen A, Muotka T (2005) Spring bryophytes in forested landscapes: Land use effects on bryophyte species richness, community structure and persistence. Biological Conservation 124: 539–545. https://doi.org/10.1016/j.biocon.2005.03.004

Hess HE, Landolt E, Müller-Hirzel R, Baltisberger M (2015) Bestimmungsschlüssel zur Flora der Schweiz und angrenzender Gebiete. Springer, Berlin, DE, 711 pp. https://doi.org/10.1007/978-3-0348-0896-5

Hinterlang D (1992) Vegetationsökologie der Weichwasserquellgesellschaften zentraleuropäischer Mittelgebirge. Crunoecia 1: 1–122.

Hinterlang D (2017). *Montio-Cardaminetea* (C6): Quell- und Waldsumpfgesellschaften. Synopsis der Pflanzengesellschaften Deutschlands 12: 1–110.

Illies J, Botosaneanu L (1963) Problèmes et méthodes de la classification et de la zonation écologique des eaux courantes, considerées surtout du point de vue faunistique. SIL Communications 12: 1–57. https://doi.org/10.1080/05384680.1963.11903811

Info Flora, the National Data and Information Center on the Swiss Flora (2020) Species distribution maps. https://www.infoflora.ch/ [accessed 12 Dec 2020]

Juillerat P, Bäumler B, Bornand C, Eggenberg S, Gygax A, Jutzi M, Möhl A, Nyffeler R, Sager L, Santiago H (2017) Flora Helvetica Checklist 2017 der Gefässpflanzenflora der Schweiz. Info Flora, Bern, CH, 380 pp.

Juutinen R (2011) The decrease of rich fen bryophytes in springs as a consequence of large-scale environmental loss. A 50-year re-sampling study. Lindbergia 34: 2–18.

Kästner M (1941) Über einige Waldsumpfgesellschaften, ihre Herauslösung aus den Waldgesellschaften und ihre Neueinordnung. Beihefte zum botanischen Centralblatt Abt. B, 61: 137–207.

Knapp R, Stoffers AL (1962) Über die Vegetation von Gewässern und Ufern im mittleren Hessen. Bericht der Oberhessischen Gesellschaft für Natur- und Heilkunde, Giessen, Naturwiss. Abt. 32: 90–141.

Küchler M (2019) Vegedaz (Version Oktober 2019). Institut für Wald, Schnee und Landschaft WSL. https://www.wsl.ch/de/services-und-produkte/software-websites-und-apps/vegedaz-version-2017.html [accessed 6 March 2020]

Küry D, Lubini V, Stucki P (2018) Verletzlichkeit von Eintagsfliegen, Steinfliegen und Köcherfliegen alpiner Quellen gegenüber Klimaveränderungen. Jahrbuch des Vereins zum Schutz der Bergwelt (München) 83: 199–218.

Küry D, Lubini-Ferlin V, Stucki P (2019) Quell-Lebensräume – Anleitung zur systematischen Erhebung und Ermittlung ihrer Bedeutung im Naturschutz. Expert report. Federal Office of the Environment FOEN, Bern, CH, 46 pp.

Landolt E, Bäumler B, Erhardt A, Hegg O, Klötzli F, Lämmler W, Nobis M, Rudmann-Maurer K, Schweingruber FH, Wohlgemuth T (2010) Flora indicativa: ökologische Zeigerwerte und biologische Kennzeichen zur Flora der Schweiz und der Alpen. 2nd edn. Haupt, Bern, CH, 378 pp.

Lubini V, Stucki P, Vicentini H, Küry D (2014) Bewertung von Quell-Lebensräumen in der Schweiz: Entwurf für ein strukturelles und faunistisches Verfahren. Expert report. Federal Office of the Environment FOEN, Bern, CH, 35 pp.

Lüth M [Ed.] (2019) Mosses of Europe – A Photographic Flora. Vol. 1–3. Michael Lüth, Freiburg, DE, 1360 pp.

Lyons MD, Kelly DL (2017) Plant community ecology of petrifying springs (*Cratoneurion*) – a priority habitat. Phytocoenologia 47: 13–32. https://doi.org/10.1127/phyto/2016/0101

Maas FM (1959) Bronnen, bronbeken en bronbossen van Nederland, in het bijzonder die van de Veluwezoom [Springs, brooks and spring forests of the Netherlands, in particular those of the Veluwezoom]. Mededeelingen van de Landbouwhogeschool 59(12): 1–166.

Meier MK, Urmi E, Schnyder N, Bergamini A, Hofmann H (2013) Checkliste der Schweizer Moose. Nationales Inventar der Schweizer Moosflora, Institut für Systematische Botanik der Universität Zürich, Zurich, CH, 31 pp.

Mogna M, Cantonati M, Andreucci F, Angeli N, Berta G, Miserere L (2015) Diatom communities and vegetation of springs in the south-western Alps. Acta Botanica Croatica 74: 265–285. https://doi.org/10.1515/botcro-2015-0024

Mucina L, Bültmann H, Dierssen K, Theurillat J-P, Raus T, Čarni A, Šumberová K, Willner W, Dengler J, …, Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19(suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Nadig A (1942) Hydrobiologische Untersuchungen in Quellen des Schweizerischen Nationalparks im Engadin. Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark 1: 267–432.

Oberdorfer E [Ed.] (1992) Süddeutsche Pflanzengesellschaften, Teil I: Fels- und Mauergesellschaften, alpine Fluren, Wasser-, Verlandungs- und Moorgesellschaften. 3rd edn. Fischer, Jena, DE, 312 pp.

Oberdorfer E (2001) Pflanzensoziologische Exkursionsflora für Deutschland und angrenzende Gebiete. 8th edn. Ulmer, Stuttgart, DE, 1051 pp.

Odum EP (1971) Fundamentals of ecology. Saunders, Philadelphia, US, 574 pp.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, …, Wagner H (2019) vegan: community ecology package. R package version 2.5-5. http://cran.r-project.org/package=vegan [accessed 12 Jun 2020]

Paton JA (1999) The liverwort flora of the British Isles. Brill, Leiden, NL, 626 pp.

Pignatti E, Pignatti S (2014) Plant life of the Dolomites. Springer, Berlin, DE, 769 pp. https://doi.org/10.1007/978-3-642-31043-0

Pott R (1995) Die Pflanzengesellschaften Deutschlands. 2nd edn. Ulmer, Stuttgart, DE, 622 pp.

Pott R, Remy D (2000) Gewässer des Binnenlandes. Ulmer, Stuttgart, DE, 255 pp.

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. 2nd edn. Cambridge University Press, Cambridge, UK, 553 pp. https://doi.org/10.1017/CBO9780511806384

R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/ [accessed 2 June 2020]

RStudio Team (2016) RStudio: Integrated Development for R. RStudio, Inc., Boston, MA. http://www.rstudio.com/ [accessed 2 June 2020]

Reiss M, Martin P, Gerecke R, von Fumetti S (2016) Limno-ecological characteristics and distribution patterns of spring habitats and invertebrates from the lowlands to the Alps. Environmental Earth Sciences 75: 1033. https://doi.org/10.1007/s12665-016-5818-8

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Schnyder N, Bergamini A, Hofmann H, Müller N, Schubiger-Bossard C, Urmi E (2004) Rote Liste der gefährdeten Moose der Schweiz. BUWAL-Reihe Vollzug Umwelt. Bundesamt für Umwelt, Wald und Landschaft BUWAL, Bern, CH, 99 pp.

Schubert R, Hilbig W, Klotz S (2001) Bestimmungsbuch der Pflanzengesellschaften Deutschlands. Spektrum Akademischer Verlag, Heidelberg, DE, 488 pp.

Sekulová L, Hájek M, Hájková P, Mikulášková E, Buttler A, Syrovátka V, Rozbrojová Z (2012) Patterns of bryophyte and vascular plant richness in European subalpine springs. Plant Ecology 213: 237–249. https://doi.org/10.1007/s11258-011-9969-0

Smith AJE (2004) The moss flora of Britain and Ireland. Cambridge University Press, Cambridge, UK, 1026 pp. https://doi.org/10.1017/CBO9780511541858

Steinmann P (1915) Praktikum der Süßwasserbiologie. I. Teil: Die Organismen des fließenden Wassers. Borntraeger, Berlin, DE, 184 pp.

Strohbach M, Audorff V, Beierkuhnlein C (2009) Drivers of plant species composition in siliceous spring ecosystems: groundwater chemistry, catchment traits or spatial factors? Journal of Limnology 68: 375–384. https://doi.org/10.4081/jlimnol.2009.375

Suanjak M (2007) Die Vegetation moosdominierter Quellfluren im Nationalpark Gesäuse. Project report for the Nationalpark Gesäuse GmbH. http://www.parcs.at/npg/pdf_public/2020/12607_20200103_095850_Suanjak2007-DieVegetationmoosdominierterQuellfluren.pdf [accessed 3 Aug 2020]

Thienemann A (1922) Hydrobiologische Untersuchungen an Quellen (I-IV). Archiv für Hydrobiologie 14: 151–190.

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Trepp W (1968) Die Pflanzengesellschaften im schweizerischen Nationalpark. Ergebnisse der wissenschaftlichen Untersuchungen im schweizerischen Nationalpark 11: 1–42.

Tüxen R (1937) Die Pflanzengesellschaften Nordwestdeutschlands. Mitteilungen der Floristisch-Soziologischen Arbeitsgemeinschaft Niedersachsen 3: 1–170.

Valachovič M [Ed.] (2001) Plant communities of Slovakia – 3. Wetland vegetation. Veda, Bratislava, SK, 434 pp.

Warncke E (1980) Spring areas: ecology, vegetation, and comments on similarity coefficients applied to plant communities. Holarctic Ecology 3: 233–308. https://doi.org/10.1111/j.1600-0587.1980.tb01226.x

Weigand E (1998) Limnologisch-faunistiche Charakterisierung von Karstquellen, Quellbächen und unterirdischen Gewässern nach Choriotopen und biozönotischen Gewässerregionen: Nationalpark o.ö. Kalkalpen, Österreich. Project report for the Nationalpark o.ö. Kalkalpen GmbH. https://www.data.gv.at/katalog/dataset/limnologisch-faunistische-charakterisierung-von-karstquellen-quellbachen-und-unterirdischen-gew [accessed 4 Jul 2020]

Wilmanns O (1998) Ökologische Pflanzensoziologie: eine Einführung in die Vegetation Mitteleuropas. 6th edn. Quelle and Meyer, Leipzig, DE, 412 pp.

Woodward G, Perkins DM, Brown LE (2010) Climate change and freshwater ecosystems: impacts across multiple levels of organization. Philosophical Transactions of the Royal Society B: Biological Sciences 365: 2093–2106. https://doi.org/10.1098/rstb.2010.0055

Zechmeister H, Mucina L (1994) Vegetation of European springs: high-rank syntaxa of the *Montio-Cardaminetea*. Journal of Vegetation Science 5: 385–402. https://doi.org/10.2307/3235862

Zemp F, Schnyder N, Danner E (2016) Moosflora des Kantons Luzern. Mitteilungen der Naturforschenden Gesellschaft Luzern 40: 1–382.

Zollhöfer JM (1997) Quellen – die unbekannten Biotope im Schweizer Jura und Mittelland: erfassen – bewerten – schützen. Bristol Stiftungsserie 6: 1–153.

Zollhöfer JM (1999) Spring biotopes in Northern Switzerland: Habitat heterogeneity, zoobenthic communities and colonization dynamics. Dissertation, Eidgenössische Technische Hochschule ETH Zurich, Zurich, CH.

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Supplementary material

Supplementary material 1
Complete relevé table and combined synoptic table
Link: https://doi.org/10.3897/VCS/2021/69101.suppl1

Supplementary material 2
Header data
Link: https://doi.org/10.3897/VCS/2021/69101.suppl2

Supplementary material 3
Environmental parameters within the seven vegetation types
Link: https://doi.org/10.3897/VCS/2021/69101.suppl3